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2020-02

Koebsch , F , Sonnentag , O , Järveoja , J , Peltoniemi , M , Alekseychik , P , Aurela , M , Arslan , A N , Dinsmore , K , Gianelle , D , Helfter , C , Jackowicz-Korczynski , M , Korrensalo , A , Leith , F , Linkosalmi , M , Lohila , A , Lund , M , Maddison , M , Mammarella , I , Mander , Ü , Minkkinen , K , Pickard , A , Pullens , J W M , Tuittila , E-S , Nilsson , M B & Peichl , M 2020 , ' Refining the role of phenology in regulating gross ecosystem productivity across European peatlands ' , Global Change Biology , vol. 26 , no. 2 , pp. 876-887 . https://doi.org/10.1111/gcb.149

http://hdl.handle.net/10138/321116
https://doi.org/10.1111/gcb.14905

unspecified
acceptedVersion

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Article type : Primary Research Articles

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Refining the role of phenology in regulating gross ecosystem productivity across European peatlands

Running title: The role of phenology in peatland GEP

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/GCB.14905

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Abstract

The role of plant phenology as regulator for gross ecosystem productivity (GEP) in peatlands is empirically not well constrained. This is because proxies to track vegetation development with daily coverage at the ecosystem scale have only recently become available and the lack of such data has hampered the disentangling of biotic and abiotic effects. This study aimed at unraveling the mechanisms that regulate the seasonal variation in GEP across a network of eight European peatlands. Therefore, we described phenology with canopy greenness derived from digital repeat

photography and disentangled the effects of radiation, temperature and phenology on GEP with commonality analysis and structural equation modeling. The resulting relational network could not only delineate direct effects but also accounted for possible effect combinations such as interdependencies (mediation) and interactions (moderation).

We found that peatland GEP was controlled by the same mechanisms across all sites: phenology constituted a key predictor for the seasonal variation in GEP and further acted as distinct mediator for temperature and radiation effects on GEP. In particular, the effect of air temperature on GEP was fully mediated through phenology, implying that direct temperature effects representing the thermoregulation of photosynthesis were negligible. The tight coupling between temperature, phenology and GEP applied especially to high latitude and high altitude peatlands and during phenological transition phases. Our study highlights the importance of phenological effects when evaluating the future response of peatland GEP to climate change. Climate change will affect peatland GEP especially through changing temperature patterns during plant-phenologically sensitive phases in high latitude and high altitude regions.

Key words: canopy greenness, mediation, moderation, structural equation modeling, commonality analysis, photosynthesis, peatland C cycle

1 Introduction

Peatlands have accumulated approximately 400-600 Gt of carbon (C) since the beginning of the Holocene and thereby exerted a significant cooling effect (Köchy *et al.*, 2015, Yu *et al.*, 2011). The climate impact of peatlands results from a small but persistent net C sink that overcompensates for the impact of sustained methane emissions (Frolking *et al.*, 2006, Frolking & Roulet, 2007). As anthropogenic global warming is projected to fuel peat mineralization rates (Dorrepaal *et al.*, 2009), the natural climate cooling effect of peatlands is increasingly challenged. Though eventually, the future development of the peatland C sink will not only depend upon greenhouse gases emitted from peat mineralization, but also upon C sequesterested via gross ecosystem productivity (GEP) and its response to a changing environment (Lund *et al.*, 2010, Oechel & Billings, 1992). Thus, detailed knowledge of the mechanisms that regulate GEP dynamics in peatlands is imperative for better predictions of the biosphere feedback to the climate system.

Phenology has recently received increasing attention as crucial driver for the peatland C cycle (Järveoja *et al.*, 2018, Kross *et al.*, 2014, Linkosalmi *et al.*, 2016, Lund *et al.*, 2010, Peichl *et al.*, 2015). Originally, phenology is defined as the timing of distinct life cycle events including the biotic and abiotic forces that regulate these recurrent dynamics (Lieth, 1975). However, with the demands of contemporary model efforts to better understand the biospheric C exchange, the concept of phenology has been expanded towards a continuous representation of plant physiological development over the course of the season (Mahadevan *et al.*, 2008, Richardson *et al.*, 2018a). In this sense, the role of plant phenology as regulator for the seasonal variation in peatland GEP is empirically not well constrained.

A mechanistic perspective on the peatland C cycle must not only incorporate the direct phenological effect on GEP but also account for potential dependencies and interactions between phenology and abiotic predictors. As phenology depends on the seasonal cycle of temperature and radiation (Russelle *et al.*, 1984), it may transmit the year-to-year variation in weather on GEP (Hollinger *et al.*, 2004, Niemand *et al.*, 2005, Richardson *et al.*, 2009). Further, phenology may modify the relationship between GEP and abiotic predictors. Such biotic-abiotic interactions can manifest, for instance, as a shifting light response function, the shape of which is modified by the availability of green biomass (Peichl *et al.*, 2018, Wilson *et al.*, 2007).

Although the linkages between biotic and abiotic predictors of GEP have been observed in different studies, the underlying relations have not been systematically compiled within a single statistical framework. Dependencies and interactions among predictor variables can be statistically described through so-called "third variable effects", namely *mediation* and *moderation* (Fig. 1). These present relational concepts that allow the effect of a predictor on an outcome to be transmitted (mediated) or modified (moderated) through a third variable (Alwin & Hauser, 1975, Baron & Kenny, 1986). Such relational concepts are well established in social and psychological sciences (MacKinnon *et al.*, 2007, Rucker *et al.*, 2011) and may also be suited to better constrain the multi-faceted effects of phenology on peatland GEP.

An independent phenological proxy is key for an explicit delineation of the abiotic and biotic effects regulating peatland GEP. Empirical approaches that describe phenology with temperature-based proxies (Alm *et al.*, 1997, Günther *et al.*, 2017, Russelle *et al.*, 1984) or CO_2 exchange measurements (Gu *et al.*, 2003, Kross *et al.*, 2014, Lucas-Moffat *et al.*, 2018, Raivonen *et al.*, 2015) may accurately reproduce phenological trajectories, but they cannot provide a mechanistic understanding of C cycling processes. Camera-based phenology metrics such as the green chromatic coordinate (GCC) measure the 'canopy greenness' derived from digital repeat photography that resolves visible changes in the RGB color spectrum over time (Richardson *et al.*, 2006, Tang *et al.*, 2016). The image archive can track greenness changes resulting from the sprouting of new plants and leaf expansion during spring green-up as well as from pigmentation change and defoliation during senescence. With its daily coverage and ecosystem-scale scope, the GCC can describe the functional effect of seasonal vegetation dynamics as key regulator for terrestrial ecosystem processes (Peñuelas & Filella, 2009, Richardson *et al.*, 2012).

The goal of this study was to unravel the mechanisms that regulate the seasonal variations in peatland GEP, with a focus on exploring the role of phenology, described by canopygreenness, versus that of abiotic predictors. For this purpose, we made use of a unique digital image archive collected across a European peatland network that co-locates digital cameras for repeat photography with net ecosystem CO_2 exchange measurements across a range of 20° latitude and 1,300m altitude. The first objective was to systematically disentangle the effects of abiotic (air temperature and photosynthetically active radiation, PAR) and biotic (canopy greenness) predictors, thereby taking into account the potential dependencies and interactions among predictor variables. The second objective was to investigate whether the identified effects change

over time, i.e. to differentiate the mechanisms regulating GEP at the start, the peak and the end of the growing season. The third objective was to assess the ubiquity of the mechanisms regulating seasonal GEP across a wide range of peatland types located in different climate regions across Europe.

2 Methods

2.1 Study sites

The peatland network includes eight European sites that span a range of 20° latitude and 1,300 m altitude across several climate regions (Fig. 2a, see also for site acronyms; Supplement S1). The contributing sites combine measurements of net ecosystem CO_2 exchange (NEE) and phenological monitoring based on digital repeat photography. For this study, available measurements from 2014 to 2016 were included and totaled 19 site years.

The dominant vegetation form at all natural peatlands are graminoids (primarily *Carex* spp., *Eriophorum vaginatum*). In addition, most sites feature an extensive Sphagnum ground cover. A few isolated trees exist at FAJ, SII and SOD (*Betula pubescens*). LAV presents a former peat extraction area after recultivation with Reed Canary Grass (*Phalaris arundinaceae*) in 2007.

2.2 Measurements of net ecosystem CO_2 exchange and auxiliary variables

Gross ecosystem productivity (GEP) is here defined as CO_2 uptake originating from primary production and was derived from the difference between the measured NEE fluxes and ecosystem respiration (Reco). All contributing sites deployed the eddy covariance technique for NEE measurements except for LAV where the closed chamber approach was used (Supplement S2). For the eddy covariance data, gap filling and partitioning of the NEE into Reco and GEP was conducted with the widely used approach of Reichstein et al. (2005). Here, Reco is modeled with an exponential temperature response curve fitted to the nighttime NEE fluxes. For LAV, Reco was directly measured with opaque chambers (Järveoja *et al.*, 2016).

Radiation and temperature data are from standard meteorological sensors mounted adjacent to, either in the same mast or in the very close vicinity according to existing protocols or praxis in the eddy covariance community (Supplement S2). Short gaps in the half-hourly PAR and temperature data were filled with linear interpolation. Larger gaps were filled with data from equivalent instruments either co-located at the same site or from another nearby site. As not each of our

member sites could provide measurements describing water availability (i.e. soil moisture or water table level), we focused on radiationand temperature as major abiotic predictors. Hence, the variance proportion in GEP attributed to water supply could not be addressed in this study.

For further analyses, we calculated daily sums for GEP and PAR (g CO_2 m^{-2} d^{-1} and mol m^{-2} d^{-1}) and daily averages for temperature (°C). All data handling was conducted in R version 3.4.3 (R Development Core Team, 2017). Time series of GEP and auxiliary variables are presented in supplement S3.

2.3 Digital Repeat Photography

Digital cameras were contained in water proof housing mounted at 2.0 to 3.8 m above the ground surface, viewing the top of the peatland canopy at shallow angles (i. e. ~15 deg). Camera azimuthal orientation was chosen to match the flux measurement footprint, and to minimize optical impairments caused by shadows and lens flare. At most sites, cameras were dismounted at the end of the growing season (November) and re-installed before the start of the following season (April-May). Images were taken at half-hourly to bi-hourly intervals, thus providing sufficient data points to compensate for weather-related scene illumination effects (Sonnentag *et al.*, 2012). Photos were saved in JPEG format. Hence, color information was converted in 8-bit red-green-blue (RGB) color code and expressed as digital numbers ranging from 0 to 255 for each color channel.

2.4 Image Analysis

2.4.1 Selection of regions of interest and calculation of chromatic coordinates

For each site, a rectangular region of interest (ROI) was selected through visual inspection of the photos (Fig. 2b). The ROI was set to capture as much of the canopy as possible, while avoiding sky or other non-representative canopy elements (e.g., instrumentation huts). Smaller, permanent structures such as boardwalks were assumed to have minor impact and were therefore not excluded from the ROIs.

We used the R package *phenopix* version 2.3.1 (Filippa *et al.*, 2017, Filippa *et al.*, 2016) to calculate ROI-averaged chromatic coordinates for the red, green and blue digital camera channels (RCC, GCC, BCC), respectively. Chromatic coordinates are derived from the ratio of the individual brightness levels to total brightness (i. e. the sum of the red, green and blue brightness levels) (Woebbecke *et al.*, 1995).

2.4.2 Filtering and aggregation of the GCC time series

The suitability of the GCC as phenological proxy depends on the selection of appropriate scene illumination conditions. For this study, we developed an automatic GCC filtering algorithm that is versatile across a range of illumination conditions and reduces the need for site-specific manual processing. In addition, a slightly modified algorithm was established to detect periods of snow cover (see supplement S4 for a detailed explanation and application examples).

In order to account for seasonal shifts in GEP predictors, we split the growing season into three phenophases:

- "green-up" defined as the period between the start of the season (SOS) and the start of the peak period (SOP),
- "peak" defined as the period between the start and end of the peak period (SOP and EOP),
- "senescence" defined as the period between EOP and the end of season (EOS).

SOS was defined as the date at which the smoothed GCC curve crossed 10% of the seasonal amplitude in spring (i.e. the GCC range spanned from the pre-season dormancy baseline to peak GCC). Analogously, EOS was defined at 10% of the seasonal range in the senescence period (from peak GCC to the post-season dormancy baseline). SOP and EOP were defined at 90% thresholds in the green-up and senescence period, respectively.

2.5 Statistical analysis

We used a two-step approach to develop and test a mechanistic model for peatland GEP. The set of potential predictor variables comprised daily aggregates of air temperature, radiation (photosynthetically active radiation, PAR) and canopy greenness as well as possible moderation and mediation effects.

In a first step, we deployed commonality analysis (CA) (Mood, 1969, Newton & Spurrell, 1967) as exploratory approach to specify the type of effect exerted through a predictor (i.e., whether a predictor operates via main, moderation and/or mediation effects). In a second step, the effects specified with CA were composed as pathways within a relational network. The constructed relational network was then tested with structural equation modeling (SEM) (Haavelmo, 1943, Jöreskog, 1970, Wright, 1921) which was here used as confirmatory approach, i.e. to support or reject the relational structures composed by the previously specified effects. To address our first objective, we conducted the analysis for an overall model aggregating over all peatlands and the

entire season. For the second objective, we repeated the analysis with a multi-group SEM that accounts for possible shifts of relations over different phenophases. Finally, to address the third objective, we set up another multi-group SEM to assess the variation of the relational structures across climate regions. CA,SEM, and the method-specific effect definitions are described in detail in supplement S5.Results

2.6 Components of explained variance in peatland GEP

When aggregated over all site-years, the combination of plant phenology (i.e., GCC), radiation (i. e., PAR), air temperature, and their interdependencies explained 70 % of the variance in the seasonal patterns of peatland GEP. Moderation effects represented through interaction terms were negligible (<1 % of explained GEP in sum) and therefore omitted from further analysis. With respect to total effects, radiation and phenology were the best predictors, each alone contributing more than 58% of the explained variance in seasonal GEP (Fig. 3). Altogether, phenology and phenology-related higher-order effects accounted for two thirds of the explained variance in GEP. Hence, only one third of the explained variance in the seasonality of GEP was attributed exclusively to abiotic effects.

Further, the excess in the total effect sum (172 %) indicated substantial collinearity among predictors, which highlights the need to further specify total effects as 1st-order unique- and higher-order mediation effects. Phenology exerted the largest unique effect (effect size 29%) and therefore constituted the most important single predictor for GEP. Among abiotic predictors, radiation constituted the largest unique effect (effect size 14 %), whilst temperature alone had virtually no effect on GEP (effect size <1 %). In sum, unique main effects contributed only 43 % to explained GEP. Hence, most of the explained variance in seasonal GEP was attributed to second-and third-order effects, mostly phenology-related mediation effects, the latter of which summed up to 48% in explained variance. Meanwhile, 9% of the explained variance in GEP could not be separated between temperature and radiation and is here referred to as common abiotic effect.

2.7 Model specification

Commonality analysis revealed substantial amounts of higher-order phenology-related effects. Hence, when relations for a mechanistic understanding of peatland CO_2 uptake are delineated, such abiotic-biotic interdependencies must be described as phenology-mediated effects. Here, we

delineated the relations suggested by CA as regression paths and tested the constructed relational network with SEM. In line with the unique radiation effect revealed by CA (14 %), we established a regression path between radiation and GEP (path Rad→GEP in Fig. 4). At the same time, we omitted such a direct regression path between temperature and GEP, as unique temperature effects turned out to be negligible. With regard to the unique effect of phenology, we established a regression path between phenology and GEP (path Phen→GEP). Further, with respect to the importance of phenology-related higher-order effects, phenology was also incorporated as outcome variable through regression paths delineated between temperature and phenology and radiation and phenology (paths Temp→Phen and Rad→Phen, respectively). Consequently, phenology was represented in a dual role as outcome and predictor variable and acted as mediator for temperature- and radiation effects on GEP. In the resulting model, radiation exerted its effect on GEP in two different ways: indirectly as predictor for phenological development and directly as predictor of the photochemical reaction rate. In contrast, temperature operated only indirectly through its effect on phenological development. As CA suggested a considerable degree of shared variance between temperature and radiation (9 %), we incorporated an undirected correlational-relation between both abiotic predictors in our SEM (represented by the double-headed arrow Rad↔Temp). We omitted any moderation effects as CA revealed their effect sizes to be negligible. The final model was over-identified with one degree-of-freedom which complies with the mathematical requirement for SEMs to permit unique estimates for all parameter.

Two additional models with the same relational structure were set up for the group-wise fitting, i.e., to assess the delineated effects for different growing seasons and climate regions. These multi-group-models were over-identified with 3 and 15 degrees-of-freedom, respectively.

2.8 Model evaluation and predictors for peatland GEP

Fit indices of the developed SEM (CFI = 98% and SRMR= 0.025, see supplement S3) suggested the hypothesized relational network to present a proper approximation for the mechanisms underlying peatland GEP and the obtained parameter estimates to be valid for interpretation. All parameter estimates were significant at an $\alpha<0.001$ level. However, due to the large sample size, we still tested for parsimony of our model to preclude single regression paths from being overrated (Sullivan et al. 2012). Therefore, we dropped the regression path with the lowest parameter coefficient and the highest relative standard error (Rad→Phen, 0.15, 12 %). The model rerun increased the Aikaike information criterion from 28,603 to 28,671. This comparison justified the

meaningfulness of the Rad→Phen regression path and further supported the entire relational network to provide the most parsimonious representation for peatland GEP.

In the final model, phenology exerted the largest effect on the seasonal variation in peatland GEP (effect size ± standard error of the path Phen→GEP: 0.59±0.02, Fig. 5), closely followed by radiation (Rad→GEP; 0.44±0.01). In turn, phenology was sensitive to temperature (Temp→Phen; 0.38±0.02), whilst the effect of radiation on phenology was subordinate (Rad→Phen; 0.15±0.02). The temperature sensitivity of phenology resulted in a distinct indirect temperature effect (Temp→Phen→GEP, i.e. the temperature effect mediated through phenology) of 0.23±0.02. In line with the subordinate role of radiation for the seasonal variation in phenology, the phenology-mediated radiation effect was low with Rad→Phen→GEP; 0.09±0.01.

2.8.1 Seasonal shift in GEP predictors

The estimated effect sizes differed distinctively among the three phenophases, thereby indicating a shift in GEP predictors over the course of the growing season (Fig. 6). During green-up, phenology was the dominant predictor for GEP with an effect size of 0.84±0.01. Radiation exerted a substantial direct effect of 0.30±0.01. Temperature affected GEP indirectly through its effect on plant growth (effect size 0.41). In addition, the model revealed a weak negative relation between phenology and radiation (-0.15±0.03).

During the peak period (i.e. the period of phenological steady state), GEP was mostly controlled directly by day-to-day variation in radiation (effect size 0.76±0.03). Direct phenology effects on peatland GEP amounted for 0.10±0.03, though this applied primarily for north boreal sites where subtle changes in greenness occur even during the peak period.

The effect patterns during senescence resembled those of the green-up period: Phenology constituted the dominant predictor for GEP, however, this biotic effect (0.61±0.01) was less pronounced than in the green-up period. Again, radiation exerted a substantial direct effect on GEP (0.40±0.01). Phenological change in the senescence period was to the same amount related to diminishing temperature and radiation (effect sizes 0.47±0.02 and 0.41±0.02, respectively).

2.8.2 Geographic variation in GEP predictors

The observed effect patterns were apparent in peatlands across all climate regions, thereby supporting the ubiquity of the found relations. However, the differences in effect sizes indicate a varying sensitivity of GEP across the spatial extent of this study. Specifically, phenology effects

on GEP were highest during green-up in northern boreal and alpine peatlands (effect sizes 0.93±0.01 and 0.93±0.03) and lowest in continental and southern boreal peatlands (0.68±0.06 and 0.74±0.03). In turn, continental and southern boreal peatlands exhibited the highest radiation effects during green-up (0.48±0.076and 0.34±0.03), whilst radiation effects during green-up of northern boreal and alpine peatlands were lowest among all climate regions (0.26±0.01 and 0.18±0.03). Radiation was the most dominant predictor of daily GEP in the phenological peak period across almost all climate regions, with highest effect sizes for north boreal and maritime peatlands (0.86±0.03 and 0.76±0.14). In addition to radiation, phenology exhibited a distinct effect on peak period GEP in north boreal sites (0.15±0.03). This indicates that subtle changes in plant activity variations during the short peak period of northern peatlands can substantially affect photosynthetic CO_2 uptake. Effect patterns in the senescence period were relatively homogenous across climate regions with effect sizes ranging from 0.38 to 0.44 for radiation and 0.55 to 0.67 for phenology.

3 Discussion

Although the importance of seasonal plant development for the peatland C cycle is well recognized, previous studies have commonly identified abiotic variables such as radiation and temperature as key predictors for the seasonal variation of peatland C fluxes (Lindroth *et al.*, 2007, Peichl *et al.*, 2014).This is because proxies to track vegetation development with daily coverage have only recently become available and due to the statistical challenge in separating potential linkages among biotic and abiotic effects. In this study, we used canopy greenness trajectories derived from digital repeat photography as continuous phenological proxy and deployed CA and SEM as statistical approaches to set up and fit a mechanistic model of peatland GEP. The relational model network performed well in reproducing the seasonal variation in observed peatland GEP. Further, although confined to a small set of regression paths, the SEM yielded essentially the same predictive power as the indiscriminate composition of all possible predictor constellations used for CA. This suggests that the empirically based delineation of observed effects provides a parsimonious and realistic representation of GEP and can thereby promote our mechanistic understanding of the peatland C cycle.

3.1 Predictors for peatland GEP

Our results support the importance of plant phenology as regulator of seasonal GEP dynamics in peatlands (Järveoja *et al.*, 2018, Linkosalmi *et al.*, 2016, Peichl *et al.*, 2018, Peichl *et al.*, 2015). Whilst these previous studies provided site-specific insights, here we demonstrate that the observed relations hold across a range of different peatlands in various climate regions. Furthermore, this study advances the mechanistic understanding of the peatland CO_2 exchange by refining the role of phenology as mediator for abiotic predictors on GEP.

Distentangling abiotic and phenological effects on the C cycle is further recomplicated by phenology itself being depenend on abiotic variables. In our study, penology was most strongly related to the seasonal cycle in mean daily temperature. In other studies, phenological development is often associated with monthly aggregated air temperature (Chen & Pan, 2002) or cumulative concepts such as heat sums (Wielgolaski, 1999). However, the scope of those studies has usually been on the prediction of distinct plant life cycle events, rather than on the transient seasonal change of phenological features. Here we observed substantial covariation between the seasonal change in canopy color and mean daily temperature. This covariation, in concert with the existing interrelation to GEP, demonstrates the tight coupling of the seasonal dynamics in temperature, phenology and peatland photosynthesis. Though, the results from our CA revealed neither a significant direct temperature effect, nor did temperature moderate the radiation effect on peatland GEP. Consequently, temperature exerted its effect on peatland GEP indirectly, i.e., through the regulation of phenological development. However, the thermoregulation of photosynthesis has been well constrained under controlled experimental conditions (Kumudini, 2004, Monson *et al.*, 1982, Sage & Kubien, 2007). Thus, our study suggests, that at ecosystem scale and under in situ conditions, direct temperature effects are superimposed, e.g. through the distinct temperature-response of phenology and/or through stronger radiation effects.

The observed interdependency between temperature and phenology justifies the utilization of temperature-based phenology proxies when the study goal is purely predictive, e. g. for CO_2 gap filling approaches and budgeting (Alm *et al.*, 1997, Günther *et al.*, 2017). Though, generic inferences about ecosystem CO_2 exchange rely on a process-based understanding and therefore on an independent incorporation of phenology in mechanistic models.

3.1.1 Seasonal shift in GEP predictors

Predictors of peatland GEP changed over the course of the growing season, thereby indicating a shift in the mechanisms regulating photosynthesis during different phenophases. During green-up, peatland GEP mostly relied on phenological development that was in turn related to rising spring air temperatures. Temperature and phenological development (e. g. represented through increases in leaf nitrogen and chlorophyll *a* concentration) are commonly known to be correlated with springtime GEP in peatlands (Moore *et al.*, 2002, Peichl *et al.*, 2015). Though here, we can explicitly incorporate the causal sequence of spring temperature rise, commencing plant growth and concurrent CO_2 assimilation in an empirical model. The fitted small negative radiation effect on springtime phenology most likely results from the specific shape of the seasonal photoperiodic curve that decreases after solstice, i.e., before the phenological peak has been reached. As radiation supply is typically not limiting photosynthesis during this time of the year, we do not interpret the fitted springtime radiation effect as causally determined.

Phenology constituted the primary predictor for peatland GEP also during senescence, though at that time of the year, phenology was not only associated with decreasing temperatures but also with diminishing radiation. Both predictors have been found to trigger the plant-physiological processes that culminate in chlorophyll degradation and the cessation of photosynthesis in experimental studies (Causin *et al.*, 2006, Rosenthal & Camm, 1997). Though recent experiments revealed minor impact of diminishing autumn radiation as fixed-term regulator for plant senescence at the end of the season (Richardson *et al.*, 2018b). Under the natural conditions of our study, diminishing autumn radiation exerted a dual effect on peatland GEP: it deprived the instantaneous photon flux supply for photosynthesis (conceptualized as direct effect) and, in concert with temperature, regulated the plant-physiological processes that initiate plant senescence (indirect, phenology-mediated effect on GEP).

3.2 Geographic variation in GEP predictors

The seasonal pattern in GEP predictors applied across all climate regions, indicating that the same mechanisms regulate peatland phenology and GEP in the northern hemisphere. Regardless, differences in effect size across climate regions should be interpreted with care: Estimates at such a high level of of group-wise fitting, can be easily confounded by site-to-site differences in productivity, vegetation type and year-to-year variation in weather (Bubier *et al.*, 1998, Linkosalmi *et al.*, 2016). Phenology was the predominant control on GEP during the green-up

phase of all climate zones. Sensitivity of GEP to spring phenology was highest in north boreal and alpine peatlands, whereas green-up GEP of more southern and low-altitude peatlands was stronger related to radiation. These geographic differences in predictors for green-up GEP could reflect phenological adaptation mechanisms as they occur across different climate regions (Howe *et al.*, 2003, Vitasse *et al.*, 2009). In alpine and northern climates, low winter temperatures can consistently suppress plant metabolic activity and induce a distinct phenological off-season. Plant growth in these regions responds rapidly to temperature rise in spring which results in a distinct green-up period with a relatively steep increase in spring GEP (Linkosalmi *et al.*, 2016, Peichl *et al.*, 2015). In comparison, more southern and low-altitude peatlands experience milder winters that allow mosses and some deciduous grass species to endure throughout the year. Without the need to renew leaf tissue at the start of the growing season, these plants can immediately start photosynthesis when radiation input increases in spring (Adkinson *et al.*, 2011).

Differences in predictors for peatland GEP during the senescence period were small and could not be attributed to climate regions. In general, the mechanisms regulating plant senescence and, as a result, autumn GEP are complex and their variation across climate regions is not well understood (Richardson *et al.*, 2013). Similar effect patterns in the senescence period of our study sites indicate the same mechanisms to regulate peatland GEP across climate regions independent from the actual timing of senescence. A more detailed understanding about the mechanisms that control senescence of peatland plants and therefore autumn GEP across climate gradients requires concerted action that complements observational studies with experimental setups (Rosenthal & Camm, 1997, Vitasse *et al.*, 2009, Wolkovich *et al.*, 2012).

Radiation was the prominent control for peatland GEP in the phenological peak period which reflects the sensitivity of photosynthesis to weather-related variation in photon flux supply during a period of phenological steady-state. This is consistent with the findings of other studies that revealed temperature and to be the best abiotic predictors for peatland GEP during the peak season(Loisel *et al.*, 2012, Peichl *et al.*, 2015). Yet, the lack of consistent water availability measurements within our network limits our model to conditions when moisture is not limiting. The rise of continental networks that base on integrated measurement protocols is promising to standardize soil moisture monitoring within the community and to better represent this parameter in future synthesis studies.

3.3 Implications for the peatland C cycle

Future development of peatlands climate impact can be best evaluated through mechanistic models that incorporate abiotic as well as biotic predictors and the linkages among them. For this purpose, our study highlights the value of incorporating a continuous phenological proxy and the existing interdependencies to major abiotic predictors within a single model framework. In doing so, our study specified the key role of phenology as mediator for abiotic effects on peatland GEP. This finding has important implications for the future development of the peatland C cycle: Under projected global warming, the C sink function of peatlands will to a large extent depend upon the temperature response of vegetation. However, as suggested by the negligible direct temperature effect on GEP, substantial changes in peatland GEP might not occur in response to warming-induced increase of CO_2 assimilation rates. Instead, our findings suggest that the essential mechanism regulating peatland GEP under global warming is based on the associated enhancement of plant growth. These plant-mediated temperature effects on GEP were constrained to phenological transition phases, primarily the green-up and, to a lesser extent, the senescence phase. This observation agrees with other findings about enhanced GEP associated with an advanced green-up in response to warmer spring temperatures (Adkinson *et al.*, 2011) and increased productivity associated with more Sphagnum growth in response to extended growing seasons (Loisel *et al.*, 2012). Hence, predictions on peatland GEP in the light of global warminig must not only focus on shifts in annual average temperatures, but especially on changing temperature patterns during plant-phenologically sensitive phases. Whilst the regulation mechanisms identified in our study, emerged across the entire range of investigated climate regions, GEP in northern and alpine peatlands was most sensitive to changes in spring phenology. In correspondence with the temperature rise expected in these regions, our study suggests global warming to raise peatland GEP especially in these climates.

To summarize, our study highlights the importance of incorporating plant phenology in observational and model studies aiming for a mechanistic understanding of the peatland C cycle. Ultimately, such a process-based understanding is a prerequisite for better predictions of biological feedbacks to the climate system.

4 Acknowledgements

FK was supported by a Postdoctoral Scholarship from the Kempe Foundation, grant number SMK-1544. FK gratefully acknowledges additional funding from the European Social Fund (ESF) and the Ministry of Education, Science and Culture of Mecklenburg-Western Pomerania within the scope of the project WETSCAPES (ESF/14-BM-A55-0030/16). Special gratitude is owed to V. Huth for his willingness to patiently comment on very early versions of the manuscript

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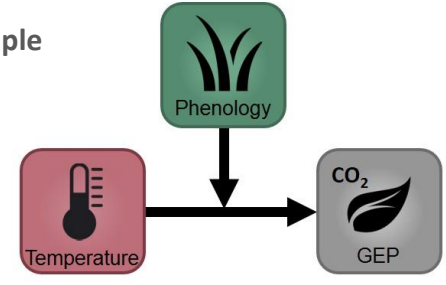
Moderation

- The strength of a predictor-outcome relation is modified by a third variable
- Assumes independence among predictors
- Commonly incorporated in multiple regression as multiplicative interaction term

Example

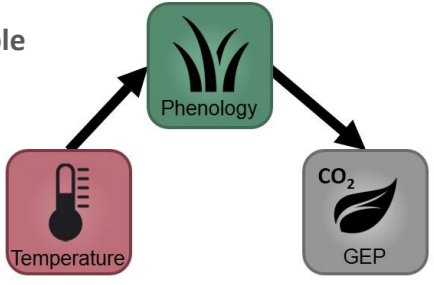


- Temperature exerts a direct effect on photosynthesis, the size of the temperature effect changes over the course of the phenological season
- Hence, phenology acts as a moderator to modify the temperature effect on photosynthesis

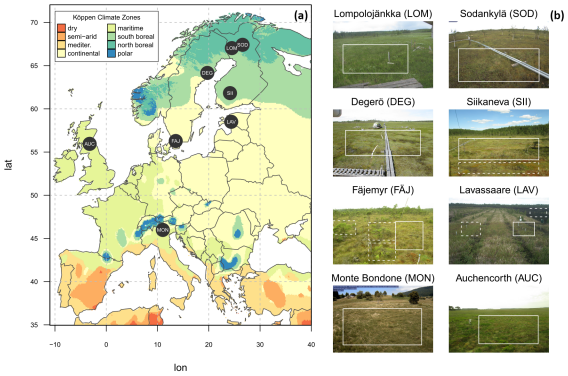
Mediation

- The effect of a predictor on an outcome is transmitted through a third variable
- Assumes interrelation among predictors
- Interrelated controls are avoided in common multiple regression settings as collinearity confounds effect size estimates

Example



- Temperature exerts an indirect effect on photosynthesis as it regulates plant phenological development which in turn regulates photosynthesis
- Hence, phenology acts as a mediator to transmit the temperature effect on photosynthesis



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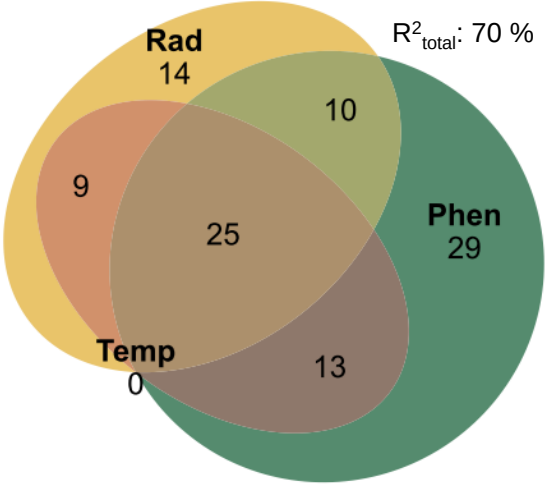
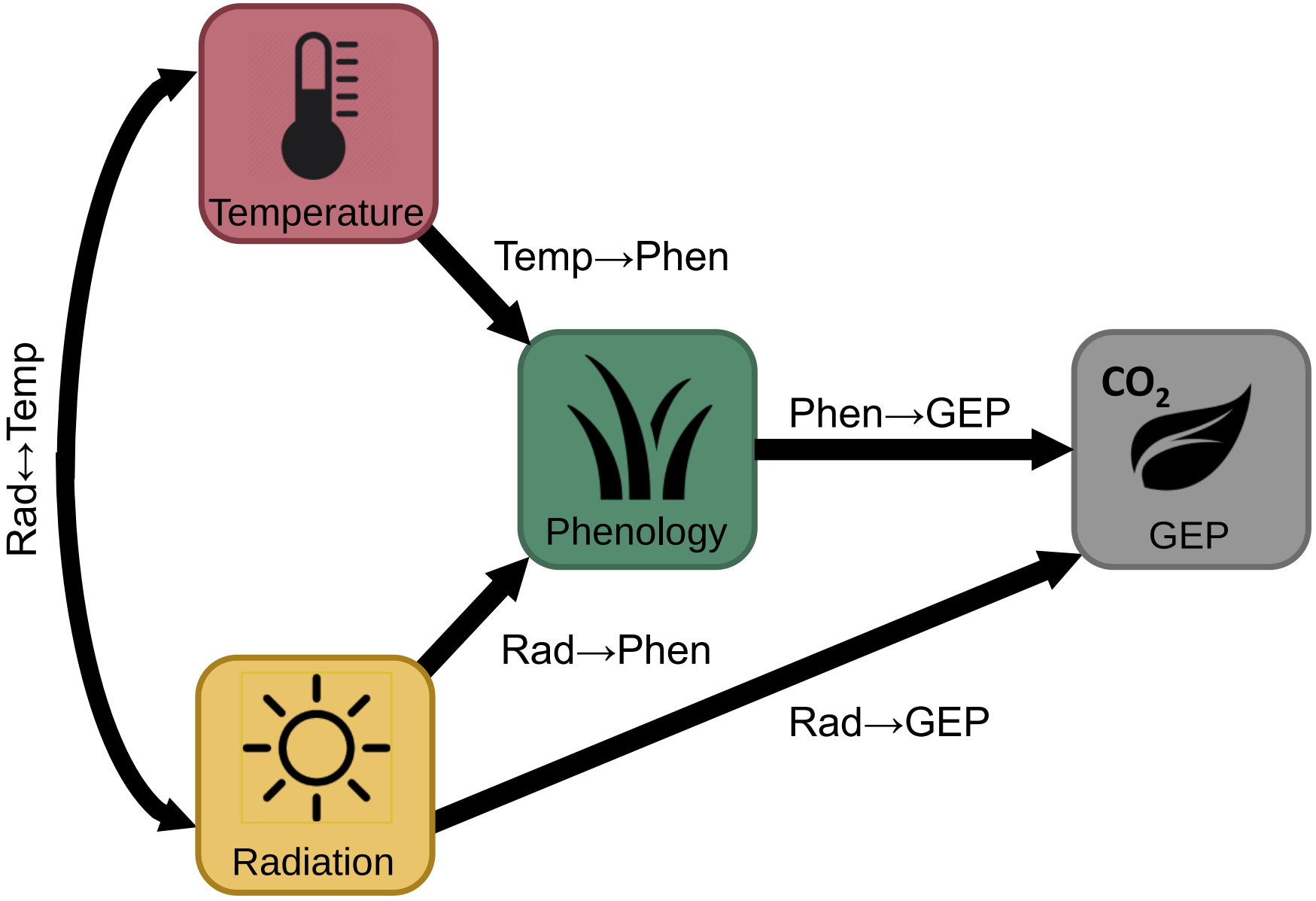
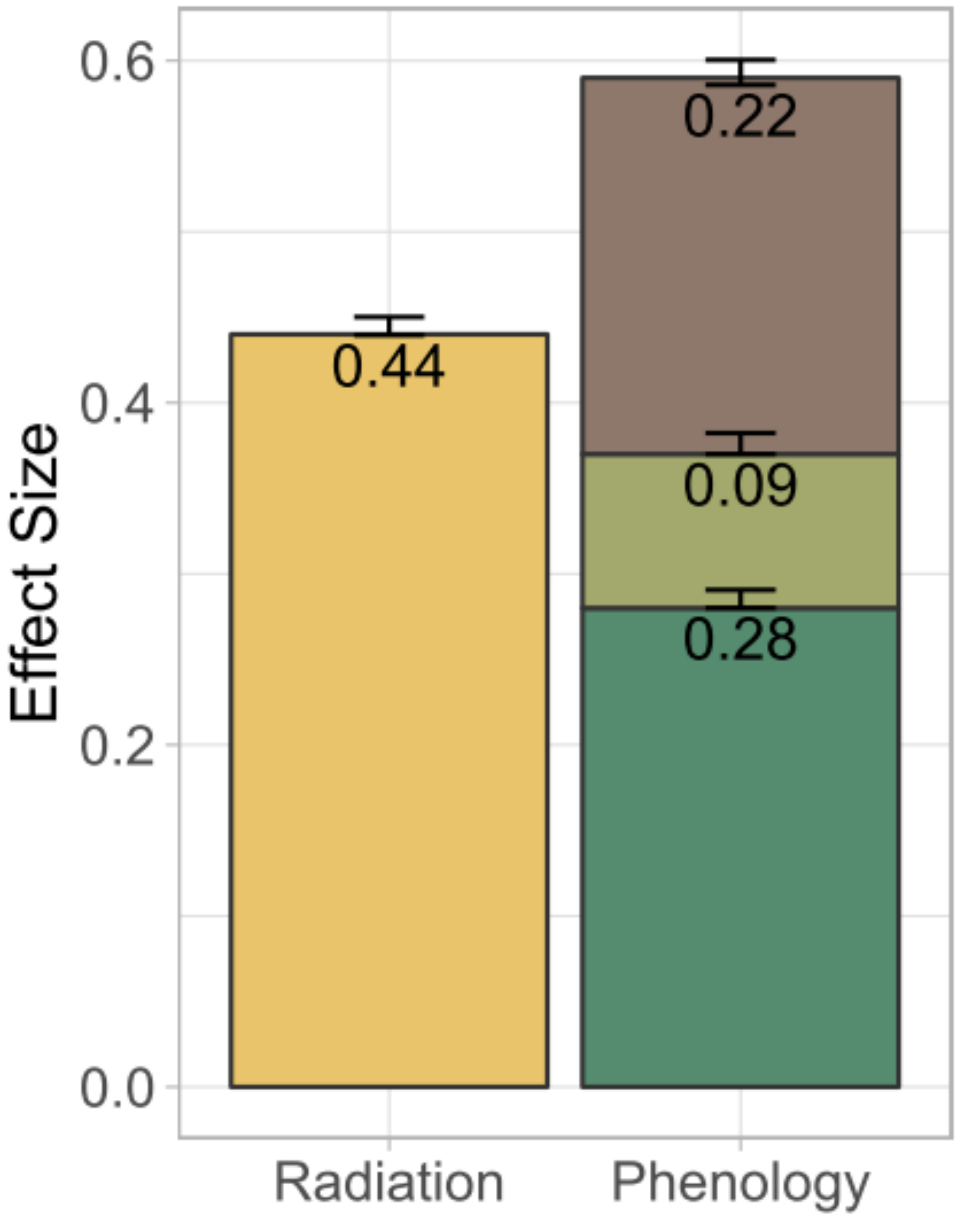
(a)



(b)

Effect type	Interpretation	Effect size in % of R^2_{total}
Total main effects		
Phen	Total phenological effect	67
Temp	Total temperature effect	47
Rad	Total radiation effect	58
		Sum: 172 %
First order unique effects		
Phen	Unique phenological effect	29
Temp	Unique temperature effect	0
Rad	Unique radiation effect	14
Second order effects		
Phen, Temp	Phenology-mediated temperature effect	13
Phen, Rad	Phenology-mediated radiation effect	10
Temp, Rad	Common abiotic effect	9
Third order effects		
Phen, Temp, Rad	Phenology-mediated abiotic effect	25
		Sum: 100 %


Temperature
Temp→Phen
Rad↔Temp
Phenology
Phen→GEP
CO_2
GEP
Rad→Phen
Rad→GEP
Radiation

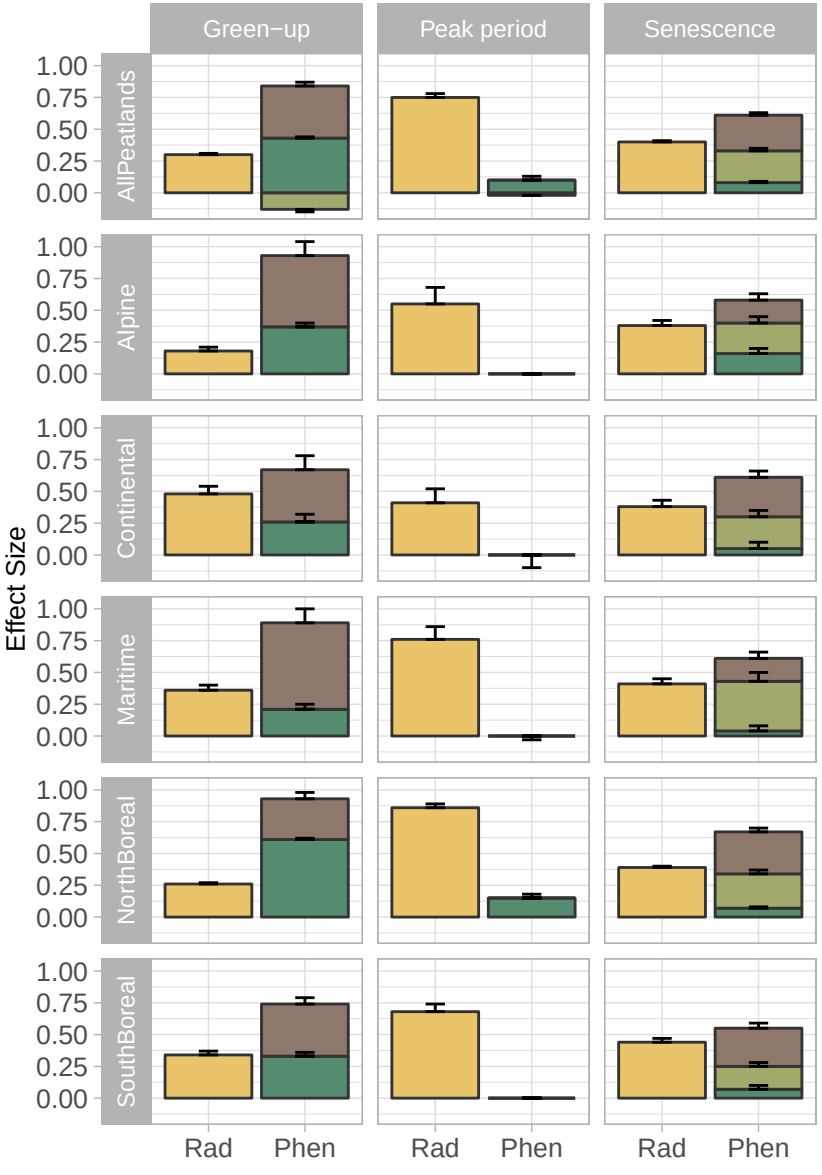


Phenology effect components

Phenology-mediated temperature effect

Phenology-mediated radiation effect

Independent phenology effect


Green−up
Peak period
Senescence
AllPeatlands
Alpine
Continental
Maritime
NorthBoreal
SouthBoreal
Effect Size
1.00
0.75
0.50
0.25
0.00
Rad
Phen